Status and trends in Arctic vegetation: Evidence from experimental warming and long-term monitoring

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Abstract

Changes in Arctic vegetation can have important implications for trophic interactions and ecosystem functioning leading to climate feedbacks. Plot-based vegetation surveys provide detailed insight into vegetation changes at sites around the Arctic and improve our ability to predict the impacts of environmental change on tundra ecosystems. Both long-term monitoring and experimental manipulation of environmental drivers (e.g. temperature) have shown impacts of environmental change, particularly climate warming, on tundra vegetation. Here, we review 30 studies of vegetation change and 12 studies of phenological change from both long-term monitoring and warming experiments in Arctic environments, including vegetation attributes identified in international assessments as monitoring priorities. General responses to natural or experimental warming include an increase in overall plant cover, particularly in the abundance of shrubs and grasses, and a decrease in lichens and mosses, but the most common abundance response was one of no change. Plant phenology often advanced in response to experimental warming, but trends over time varied by site, species, and phenostage. This synthesis demonstrates that Arctic plant communities and species are generally sensitive to warming, but trends over time are heterogeneous and complex and do not always mirror expectations based on responses to experimental manipulations. Our findings highlight the need for more geographically widespread, integrated and comprehensive monitoring efforts that can better resolve the interacting effects of warming and other local and regional ecological factors.

Keywords

vegetation change, phenology, Arctic, experimental warming, long-term monitoring

Introduction

A major goal of global change ecology is to document and predict the impacts of environmental change on species, communities and ecosystems worldwide. In the Arctic, exceptionally rapid warming (IPCC 2013) has the potential to lead to dramatic changes in vegetation through longer growing seasons, increased thaw depth, and altered snow regimes. High latitudes contain up to 50% of the world's soil carbon stored in permafrost soils; this carbon is vulnerable to loss with warming (Schuur et al. 2015; Crowther et al. 2016; van Gestel et al. 2018). Thus, change in vegetation carbon and nutrient inputs to tundra soils could have potentially global impacts. For example, shifts in species composition could lead to changes in aboveground carbon storage, nutrient cycling,

decomposition rates, and albedo (Callaghan et al. 2004), potentially leading to global climate feedbacks (Chapin et al. 2005; Pearson et al. 2013). Changing vegetation could also alter trophic interactions (Post et al. 2009; Gauthier et al. 2013) and thus influence Arctic wildlife populations and the human communities that rely on them for resource provision or cultural purposes (Weller et al. 2004; Henry et al. 2012; Stern and Gaden 2015).

A key source of information about the consequences of climate warming for Arctic vegetation comes from plot-based research at sites across the Arctic (Henry and Molau 1997). This includes both long-term monitoring of species composition, diversity, and phenology over time (up to four decades), as well as experimental manipulation of key abiotic and biotic drivers (e.g., temperature, snow, nutrients, grazing). Community composition, diversity, and phenology have all been identified as "Focal Ecosystem Components" (FECs) by the international Circumpolar Biodiversity Monitoring Program (Christensen et al. 2013), as monitoring of these attributes facilitates a more rapid detection, communication, and response to significant biodiversity-related trends and pressures affecting the circumpolar world. In addition, comparing the results of observed trends over time with experimental studies can help to elucidate the drivers of observed trends and inform predictions of future change (Elmendorf et al. 2015).

Here, we synthesize what is currently known about plot-based changes in vegetation composition (abundance), phenology, diversity, and functional traits. We compiled information from single-site studies of composition and phenological change to document 1) the direction and significance of change over time, and 2) the direction and significance of responses to experimental warming. We compare these results to published syntheses of long-term monitoring and experimental warming. We additionally review studies of plot-based changes in plant functional traits and diversity, for which published observations are relatively scarce. Finally, we discuss the broader implications of observed and predicted Arctic vegetation change and recommend priorities for future monitoring efforts.

Materials and Methods

Literature review of vegetation trends

We conducted a literature review to identify single-site studies of changes in plant community composition (abundance) and phenology both over time and in response to experimental warming. Our search included combinations of the terms "tundra", "arctic", "vegetation", "plot", "change", "ITEX", "cover", "abundance", "phenology", "diversity", "functional trait", "warming", and "experiment". These terms encompasses two Focal Ecosystem Components included in the Circumpolar Biodiversity Monitoring Program terrestrial monitoring plan: i) diversity, composition

and abundance and ii) phenology. We do not include the attributes “diversity and spatial structure”, “productivity”, “Rare species, species of concern”, or “food species” in this review due to a paucity of published plot-based monitoring and/or experimental studies on these topics. The attribute “non-native species” is addressed in a separate article in this issue [WASOWICZ ET AL., THIS ISSUE].

We included only studies at sites above 63 °N and identified as “Arctic” or “tundra” by the authors. This latitudinal cut-off includes some sub-Arctic sites but is roughly comparable to areas included in the Arctic Biodiversity Assessment (CAFF 2013 2013). For community composition/abundance, we included measured responses in any variable called abundance, biomass, or percent cover. We included studies that analyzed changes in abundance at both the species and functional group level. For studies where abundance trends were identified at the species level, we included all species but grouped them by functional group for visualization purposes. All phenological responses were provided at the species level.

For phenological studies, we recorded all phenostages provided by the authors, but here we report only the most commonly observed phenostages: leaf emergence, flowering, and leaf senescence. Leaf emergence is the day at which leaf bud-break first occurs or the first day on which overwintered leaves re-green. Flowering encompasses several phases related to the timing of flowering, including inflorescence elongation, first open flower, onset of pollen release, and peak flowering. Leaf senescence is the date on which leaves change color or die, indicating the end of the growing season for most plants. Studies reporting responses of diversity and/or functional traits were scarce; thus, we review the available information but do not attempt to categorize and quantify these responses.

For all studies we recorded the direction (increase/stable/decrease for abundance change, or earlier/stable/later for phenological change) and significance (yes/no) of responses for all species and functional groups identified. A response could be recorded as directional (increase/decrease or earlier/later) and non-significant if the authors identified it as such, or if the p-value provided was between 0.05 and 0.1. We adopted this approach in order to standardize alpha levels across all studies (e.g. if some studies used an alpha level cut-off of 0.05 to assess significance while others used an alpha level of 0.1). If a response was identified by the authors as directional but no indication of significance was given (either in the text or in a figure/table), the response was categorized as non-significant. The difference between significant and non-significant directional changes is shown in the figures and provided in the supplementary data table. We used this “vote-counting” approach, rather than a traditional meta-analysis, in order to include the many studies that do not provide response effect sizes or estimates of error. In addition, this approach allows us to visualize the full distribution of vegetation responses to ambient and experimental warming, as a meta-analysis finding of “no-

change" could in fact be made up of multiple significant changes in different directions (e.g. context dependency).

Experimental warming was generally conducted through the use of clear-sided, open-top chambers that passively warm air temperatures by ~1.5-3 °C, with most of the studies following International Tundra Experiment (ITEX) protocols (Molau and Mølgaard 1996; Marion et al. 1997), though some experiments used greenhouses or other warming methods (Chapin and Shaver 1996; Wang et al. 2017). The seasonal duration of warming also varies by study; some warming chambers were in place only during the summer, while others were present year-round. Both warming chambers and greenhouses can influence environmental factors other than temperature (e.g. soil moisture, wind, snow accumulation), though the magnitude and significance of these effects are variable among sites (Marion et al. 1997).

Comparison to tundra-wide syntheses

In order to evaluate the consistency of patterns revealed by the literature review, we compared the results of our review with tundra-wide syntheses of community composition and phenological change (Arft et al. 1999; Walker et al. 2006; Elmendorf et al. 2012a; Elmendorf et al. 2012b; Oberbauer et al. 2013), both over time and in response to experimental warming. These syntheses used primary data and were not based on published studies, though some data included in the syntheses may be from the same sites as the single-site studies included in our literature review. However, the synthesis and single-site studies likely include different combinations of sites and years, and use different statistical methods to analyze responses. In addition, many of the synthesis studies included both Arctic and alpine tundra sites, while here we focused exclusively on Arctic and sub-Arctic locations. Thus, evidence that synthesis studies found trends consistent with those documented in this literature review can help evaluate the robustness of observed patterns in Arctic vegetation change.

Results

We identified a total of 560 vegetation composition/abundance observations (species or functional group) from 19 studies of long-term monitoring and 209 observations from 14 studies of responses to experimental warming (Figure 1, Table 1). The duration of monitoring studies ranged from five to 43 years, with a median duration of 19 years. We additionally identified long-term monitoring of phenology for 17 species in three studies and responses to experimental warming of 52 species from nine studies (Figure 1, Table 1). Phenological monitoring studies ranged from nine to 21 years in duration, with a median duration of 16 years.

Our literature review reveals geographical gaps in both long-term monitoring and experimental warming studies. The FEC (Christensen et al. 2013) encompassing composition and abundance is better represented than that encompassing phenology, but both lack published records of change from Siberia and wide swaths of the Canadian Arctic. Intensive, multivariate monitoring is concentrated primarily in Alaska and Scandinavia, with the exception of one site in high-Arctic Canada (Muc et al. 1989; Freedman and Svoboda 1994; Hudson and Henry 2009; Hill and Henry 2011; Bjorkman et al. 2015).

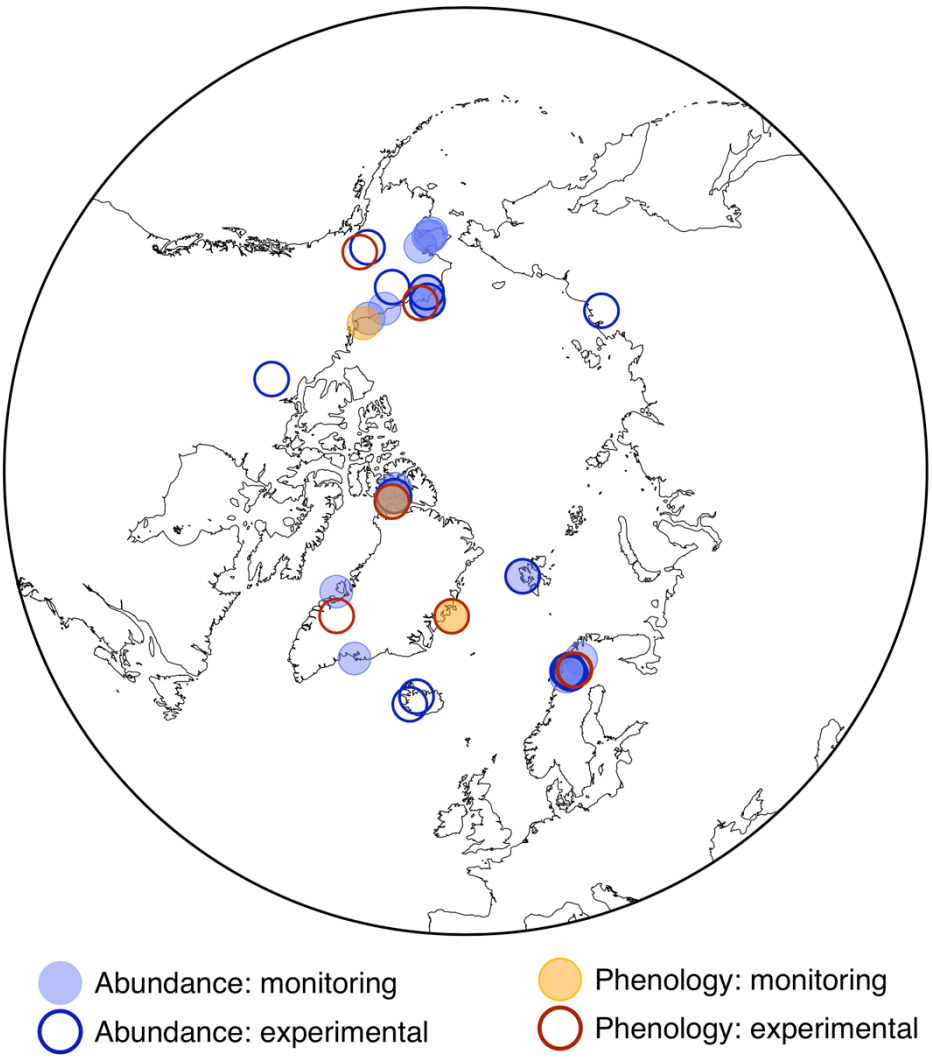

Figure 1. Map of plot-based vegetation change studies identified in a review of the literature. Blue points designate studies of community composition (abundance) change, while orange points designate studies of phenological change. Filled circles denote long-term monitoring studies (change over time) while open circles indicate experimental studies (responses to experimental warming).

Vegetation composition change

In all cases, the most common response documented by long-term monitoring of compositional change was one of no trend (52-84% of trends did not differ from zero, depending on the significance

cutoff used; Figure 2). This is likely an underestimate of the proportion of no-change responses, as some studies reported results only for species that changed significantly over time (Tømmervik et al. 2004). Forbs, graminoids and both evergreen and deciduous shrubs were slightly more likely to increase in abundance over time than decrease, but were most likely to remain stable. Experimental warming led to more dramatic responses, particularly in lichens, which were far more likely to decrease in abundance in response to experimental warming (46-63%) than to increase (0%) or remain stable (37%). Bryophytes also had a tendency to respond negatively to experimental warming, while evergreen and deciduous shrubs were more likely to respond positively.

Few studies included both above- and below-ground measurements; of those that did, above- and below-ground responses were not always consistent. Above-ground responses to experimental warming in northern Alaska were greater than below-ground responses (Chapin and Shaver 1996), but below-ground biomass increased more than above-ground biomass over 30 years of monitoring at Alexandra Fiord, Ellesmere Island (Hill and Henry 2011). At Daring Lake, Canada, experimental warming enhanced both above- and below-ground biomass in evergreen shrubs, but only above-ground biomass in deciduous shrubs (Zamin et al. 2014).

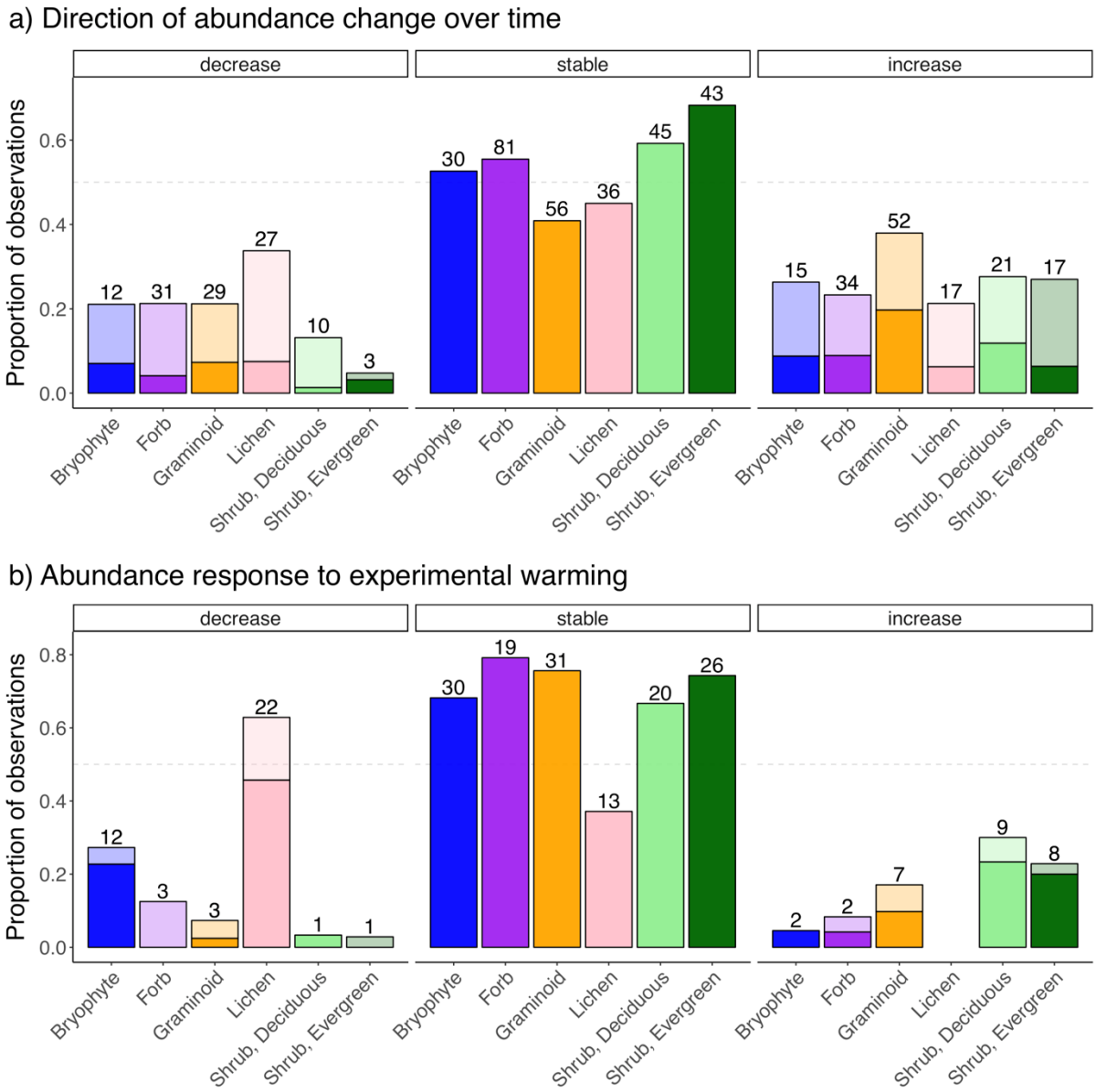

Figure 2. Summary of studies investigating abundance change over time (a) and abundance change in response to experimental warming (b) by species or functional group. Panels represent, from left to right, the proportion of observations decreasing in abundance, stable, or increasing in abundance over time (median 20.5 years) or in response to experimental warming. Species-specific trends were grouped into the relevant functional group category. The darker portions of each bar represent "significant" ($p < 0.05$) change (decrease or increase) or insignificant (stable; $p > 0.1$) results, while lighter colors represent borderline or marginally significant change (e.g., p-values between 0.05 and 0.1). The numbers above each bar represent a count of the number of observations included in that group. The proportion of "stable" species is underrepresented in this figure, as some studies only reported results for species that changed in abundance.

These responses are largely in line with those revealed in tundra-wide syntheses of vegetation change at the functional group level. In a recent thirty-year study of vegetation change across 46 Arctic, alpine and Antarctic tundra locations (Elmendorf et al. 2012b), only evergreen shrubs (but not deciduous) increased significantly over time. Bryophytes were more likely to decrease than increase, but the response was not significant. Similar to results from our literature review, responses to experimental warming were more dramatic. Deciduous but not evergreen shrubs increased

198 significantly in abundance in response to experimental warming, while both lichens and bryophytes
199 decreased significantly (Elmendorf et al. 2012a). In both monitoring and experimental synthesis
200 studies, the quantity of dead material (litter and attached dead) increased over time or with warming
201 (Elmendorf et al. 2012a; Elmendorf et al. 2012b).
202
203 *Phenological change*
204 In general, the timing of leaf emergence and flowering advanced both over time and with
205 experimental warming, though a minority of species experienced stable or even delayed flowering
206 over time (Figure 3). Interestingly, experimental warming led to later leaf senescence in all cases,
207 while the one study that documents long-term trends in leaf senescence (Myers-Smith et al. 2018)
208 found a non-significant trend toward earlier leaf senescence over 16 years of monitoring.
209

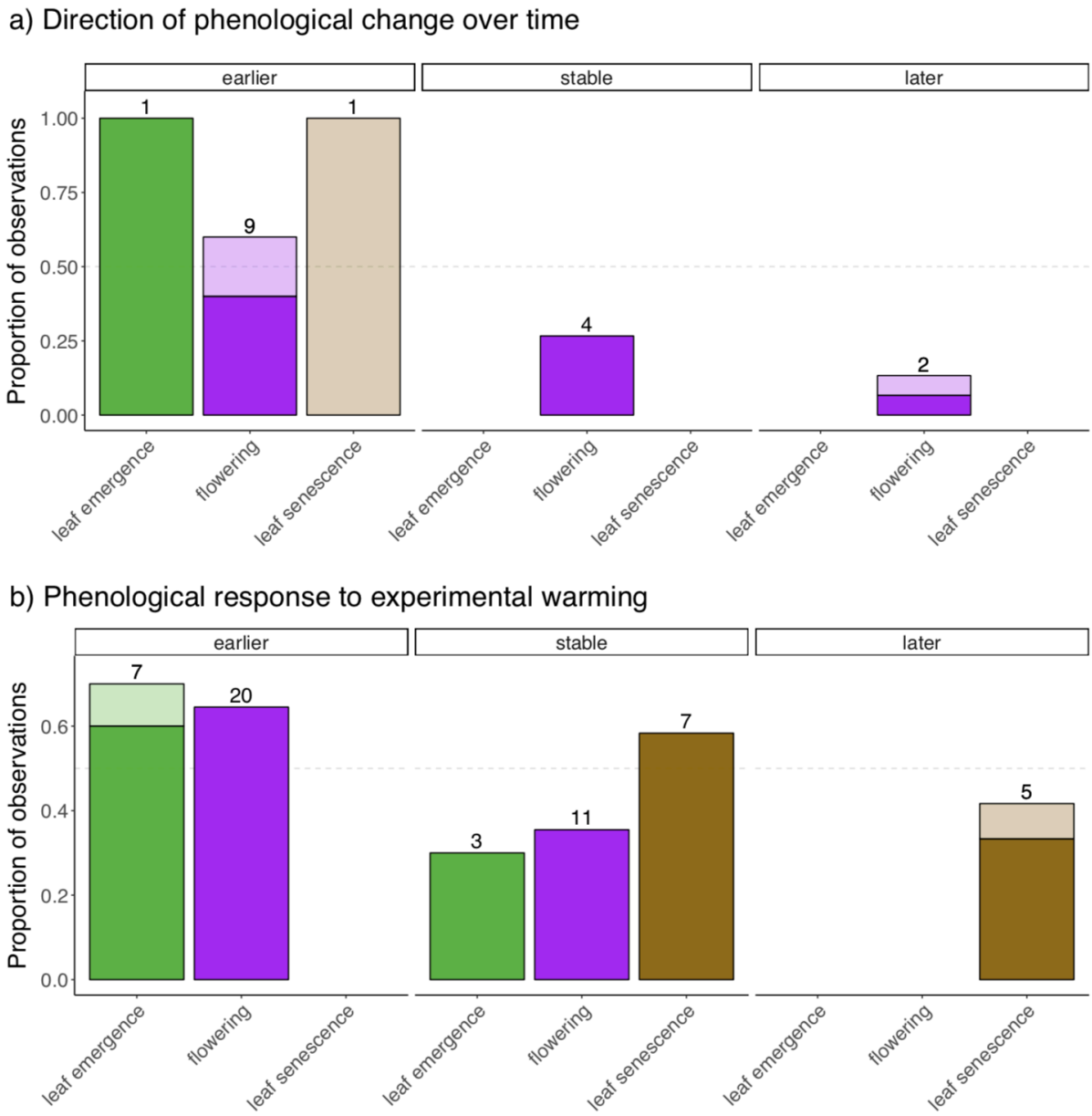

Figure 3. Summary of studies investigating phenological change over time (a) and in response to experimental warming (b). Panels represent, from left to right, the proportion of observations that advanced ("earlier") in a given phenological stage, remained stable, or were delayed ("later") over time or in response to experimental warming. All observations represent species-specific responses. The darker portions of each bar represent "significant" ($p < 0.05$) change (decrease or increase) or insignificant (stable; $p > 0.1$) results, while lighter colors represent borderline or marginally significant change (e.g., p-values between 0.05 and 0.1). The numbers above each bar represent a count of the number of observations included in that group.

In a 17-year synthesis of phenological trends at 12 tundra sites (including two alpine locations), there was no significant change in the timing of flowering or leaf senescence, though both events tended to advance over time (Oberbauer et al. 2013), as we also found in the literature review. Surprisingly, this same synthesis study found that leaf emergence was significantly delayed over time despite increasing temperatures over the same period. In a separate synthesis of responses to experimental warming at 10 Arctic sites, leaf emergence and flowering both occurred significantly earlier when warmed, but

senescence was not affected (Arft et al. 1999). This is also in agreement with our literature review, where most sites reported no difference in leaf senescence or a slight delay.

Discussion

Studies of plot-based vegetation change reveal that while some sites and species or functional groups have experienced substantial shifts in vegetation and phenology in response to ambient or experimental warming, the most common response overall is one of no change. Furthermore, vegetation changes over time did not always match responses to experimental warming. One pattern emerges: both long-term monitoring and experimental studies suggest that the graminoid and shrub functional groups respond positively to warming and are slightly more likely to increase in abundance over time. This is in line with studies of shrub infilling and expansion across much of the tundra (Sturm et al. 2001; Myers-Smith et al. 2011a; Martin et al. 2017). Even so, the majority of graminoid and shrub abundance responses in our literature review were that of no significant trend over time and no significant response to experimental warming. Further exploration of these trends reveals that increasing shrub abundance primarily occurs in relatively warm tundra regions with mesic or wet soils, while colder and dry tundra sites have not experienced increasing shrub abundance (Elmendorf et al. 2012b) consistent with patterns in the climate sensitivity of shrub growth (Myers-Smith et al. 2015). Grazing may also influence shrub responses to summer temperature change (Bråthen et al. 2017).The lack of strong trends over time in many sites and for many species suggests that tundra plant communities are remarkably resilient to moderate warming, at least over decadal time spans, and that site-specific factors such as moisture availability and grazing may limit vegetation responses to warming (Elmendorf et al. 2012b; Myers-Smith et al. 2015; Ackerman et al. 2017).

Differing responses to experimental and ambient (natural) warming highlight both the benefits and the challenges of using experimental approaches to understand tundra vegetation responses to climate change. When experimental and monitoring results agree, experimental studies enable us to pinpoint the likely drivers of change over time (Elmendorf et al. 2015), and improve our confidence in predictions of the impacts of warming on vegetation (e.g., increasing shrub abundance). Diverging responses can challenge our understanding of tundra vegetation change. For example, while experimental warming led to fairly dramatic declines in lichen abundance (Walker et al. 2006; Elmendorf et al. 2012a and this study), lichen abundance did not decline over time in long-term monitoring studies (Elmendorf et al. 2012b and this study). Similarly, while experimental warming generally led to later leaf senescence (Arft et al. 1999 and this study), monitoring studies indicate that senescence is in fact advancing over time, though not significantly (Oberbauer et al. 2013 and this study). Trends in the timing of flowering and leaf emergence are also varied despite a relatively consistent advance in these variables in response to experimental warming.

The reasons underlying these heterogeneous and contrasting trends are not entirely clear, but may have to do with interactions among environmental drivers that are not captured by experimental isolation of a single driver. For example, lichens are sensitive to soil moisture, and may be responding to changes in precipitation, hydrology, or snow regimes over time rather than temperature trends alone (Björk and Molau 2007). Similarly, phenological advance with warming temperatures (Høye et al. 2007) may be limited by concurrent changes in winter snowfall (Bjorkman et al. 2015) and snowmelt date (Cooper et al. 2011). In addition, growing season phenology might be controlled by deterministic leaf age (Starr et al. 2000) or adaptation to photoperiod (Kummerow 1992; Bjorkman et al. 2017) in many Arctic species, thus limiting the impact of temperature change alone. Phenological responses to different drivers may interact or be non-linear, leading to more complex responses than can be easily detected from simple experiments or ecological monitoring studies (Iler et al. 2013). Finally, experimental warming chambers can alter conditions other than temperature alone (Marion et al. 1997), and vegetation could be responding to these unwanted environmental side-effects.

Improved monitoring of multiple environmental drivers and experimental studies that manipulate several variables simultaneously (e.g. snow depth, moisture availability) could help to elucidate the importance of these interactions. Multi-site syntheses can also help to clarify the context dependency of trends over time. For example, additional syntheses of tundra plant phenology have shown that a plant's sensitivity to temperature varies by the temperature of the site (greater sensitivity at colder sites; Prevéy et al. 2017) as well as the phenological niche of the species (greater sensitivity in late-flowering species; Prevéy et al. 2018).

Other vegetation trends: functional traits and diversity

While trends in composition and phenology are perhaps the most studied plot-based responses to global change, a handful of studies document changes in other vegetation parameters. Of these, increasing height is likely the most well-documented. Increases in community height have been documented by synthesis studies of responses to experimental warming (Elmendorf et al. 2012a) and over time (Bjorkman et al. 2018), a change driven primarily by the influx of taller species into the monitoring plots (Bjorkman et al. 2018). Some single-site studies have also documented increasing height over time (Hollister et al. 2015) and in response to experimental warming (Hudson et al. 2011; Hollister et al. 2015; Baruah et al. 2017). Changes in other plant traits have also been documented. Experimental warming at Alexandra Fiord in high Arctic Canada resulted in greater leaf size, lower specific leaf area (the ratio of leaf area to leaf dry mass), and decreased leaf carbon content for at least some species-site combinations (Hudson et al. 2011) but did not affect leaf nitrogen (N) content, leaf dry matter content, or nitrogen isotope signatures. Other studies have documented mixed responses of

leaf size to experimental warming in the Swedish subarctic tundra (Graglia et al. 1997; Baruah et al. 2017) and one study found trends toward reduced leaf size over time (Barrett et al. 2015). Additional studies of leaf N content responses to experimental warming are also mixed; leaf N content increased in response to winter but not summer warming across six species at Eight Mile Lake, Alaska (Natali et al. 2012) but was either unaffected by temperature or declined in response to warming at Toolik Lake, Alaska (Chapin and Shaver 1996) and Alexandra Fiord, Canada (Tolvanen and Henry 2011). A synthesis of community-weighted mean functional trait change across the tundra biome (including alpine sites) over 27 years found no significant change in leaf area, leaf N content, leaf dry matter content, or specific leaf area (Bjorkman et al. 2018). Overall, species composition has shifted toward more thermophilic (warm-loving) species both over time and in response to experimental warming (Elmendorf et al. 2015).

Over the long term, climate warming may lead to increased diversity in the Arctic as southern, species-rich floras move northward (Parmesan 2006). However, short-term responses to warming might differ substantially from long-term trends, as immigration is likely to be slow relative to local assembly processes (e.g. competition; Walker et al. 2006). Thus far, evidence of plot-scale diversity change in Arctic ecosystems is mixed. A multi-site synthesis found a significant decline in both Shannon diversity and species richness after three to six years of experimental warming (Walker et al. 2006), but a more recent, longer-term synthesis found no response (Elmendorf et al. 2012a). Lichen diversity was found to decline significantly in response to long-term experimental warming at three sites in northern Sweden and Alaska (Lang et al. 2012). Among monitoring studies, a recent synthesis found no change in vascular plant diversity over three decades of monitoring across dozens of tundra sites (Elmendorf et al. 2012b). This is in stark contrast to ongoing changes in European mountaintop plant communities, which have experienced rapid and accelerating increases in richness over the past century (Steinbauer et al. 2018). This difference could indicate that diversity change in non-alpine tundra communities is limited by dispersal rates of southerly, warm-adapted species, or that strong gradients in environmental variables other than temperature (e.g. photoperiod) across latitudes limit the establishment success of warm-adapted species from farther south (Bjorkman et al. 2017).

Consequences of Arctic vegetation change

Changes in tundra vegetation could have far-reaching impacts across trophic levels and to human societies (Weller et al. 2004). Shifts in plant phenology and reproductive success influence individual- and population-level fitness (Berteaux et al. 2004; Cleland et al. 2012) and could lead to trophic mismatches of resources for pollinators (Høye et al. 2013; Wheeler et al. 2015; Prevéy et al. 2018), breeding birds (McKinnon et al. 2012; Gauthier et al. 2013; Boelman et al. 2015) and mammals (Hertel et al. 2017). For example, one long-term study at Zackenberg, Greenland documented a

shortening of the flowering season with climate warming over time and a concurrent decline in the abundance of insect visits to flowers (Høye et al. 2013). Berry-producing (Hertel et al. 2017) and other tundra plants provide forage for hunted or domestic wildlife (Post and Stenseth 1999; Kerby and Post 2013) and represent culturally important resources for Arctic peoples (Henry et al. 2012).

The nearly ubiquitous shifts in phenology in response to experimental warming (Arft et al. 1999 and this study) suggest that many Arctic plant species are inherently sensitive to interannual variations in temperature, though concurrent changes in other environmental variables (e.g. precipitation, cloudiness) might limit the degree of advance over time with warming. A meta-analysis of phenological responses to experimental warming in temperate and alpine regions found that the temperature sensitivity of a species' phenology correlates with better growth and/or reproductive performance (Cleland et al. 2012), but it is not known if this pattern holds true in the Arctic. A synthesis of responses to four years of experimental warming at 10 Arctic sites revealed increased reproductive effort (e.g. number of flowers produced) and success (e.g. number of seeds/fruits produced or seed mass) in experimentally warmed plots, though responses were generally not significant (Arft et al. 1999). Single-site studies have also found evidence of increased reproductive effort in experimentally warmed plots (Welker et al. 1997; Klady et al. 2011). Contrasting responses have been documented for seed germination rates, which increased with experimental warming at Alexandra Fiord, Canada (Klady et al. 2011) but not at Toolik Lake, Alaska (Welker et al. 1997).

Due to the large amount of carbon stored in tundra permafrost soils (Koven et al. 2011; Schuur et al. 2015; Crowther et al. 2016) and well-established links between vegetation and carbon storage, vegetation change in the Arctic can influence regional carbon cycling and feedbacks to the global climate (Callaghan et al. 2004; Sturm and Douglas 2005; Petrenko et al. 2016). For example, increasing shrub abundance and/or plant height can lead to increased winter snow trapping, greater insulation of underlying soils, warmer winter soil temperatures (Myers-Smith and Hik 2013), and potentially increased active layer depth and decomposition (Blok et al. 2016). Taller shrubs may also extend above the snowpack, decreasing winter albedo and increasing absorbed solar radiation (Sturm and Douglas 2005). Bryophytes have also been shown to play an important role in soil insulation and energy fluxes; experimental removal of bryophytes leads to increased evapotranspiration and ground heat flux (Blok et al. 2011). Thus, future declines in bryophytes – observed in warming experiments but not yet in monitoring studies – could also lead to deeper summer permafrost thaw and soil carbon release, representing another positive feedback to climate warming.

Changing vegetation can also impact carbon cycling through changes in the quantity and decomposability of litter (Callaghan et al. 2004), as litter decomposition contributes nearly 70% of global CO_2 fluxes from soils (Raich and Potter 1995). A long-term increase in shrubs, which have

relatively recalcitrant litter, could lead to reduced litter decomposability and a negative feedback to climate warming (Cornelissen et al. 2007). A change in litter composition can also indirectly influence soil carbon storage by driving changes in soil microbial communities (Christiansen et al. 2018) or altering tundra fuel loads. For example, increased woody litter inputs from shrub expansion might also increase flammability, which could lead to positive feedbacks through fire-induced soil carbon loss (Cornelissen et al. 2007; van Altena et al. 2012).

Conclusions

Rapid warming in the Arctic has the potential to cause substantial shifts in vegetation, potentially driving widespread changes across trophic levels and altering tundra ecosystem functions. While our review identifies significant shifts at some sites and in some species, the large variation in the magnitude and even direction of responses illustrates the high degree of context dependency in tundra vegetation change. This context dependency highlights the importance of maintaining multiple monitoring sites in many different habitat types across the entire Arctic, as well as increasing monitoring of local ecological and environmental conditions that would improve our understanding of how factors other than temperature influence Arctic vegetation change. Thus, we recommend that international bodies such as the Circumpolar Biodiversity Monitoring Program (Christensen et al. 2013) prioritize monitoring efforts that i) fill current geographical gaps, particularly in Canada and Siberia, and ii) enable us to better disentangle the relative importance of climate warming and other environmental factors on the diverging responses reported here.

394 *Table 1. Studies of abundance and phenology included in this review.*

					Abundance		***Phenology***	
Study	**Site name**	**Lat**	**Lon**	**Duration (years)**	**monitoring**	**experiment**	**monitoring**	**experiment**
(Alatalo and Totland 1997)	Latnjajaure, Lapland, Sweden	68.21	18.3	1				x
(Bjorkman et al. 2015)	Alexandra Fiord, Ellesmere Island, Canada	78.53	-75.55	21			x	x
(Boulanger-Lapointe et al. 2014)	Alexandra Fiord, Ellesmere Island, Nunavut	78.86	-75.9	13-15	x			
(Boulanger-Lapointe et al. 2014)	Sverdrup Pass, Ellesmere Island, Nunavut	79.13	-79.73	5-23	x			
(Callaghan et al. 2011)	Disko Island, Greenland	69.15	-53.34	43	x			
(Chapin and Shaver 1996)	Toolik Lake, Alaska	68.38	-149.34	4		x		
(Chapin et al. 1995)	Toolik Lake, Alaska	68.38	-149.34	9		x		
(Daniëls and de Molenaar 2011)	Tasiilaq, Southeast Greenland	65.62	-37.67	41	x			
(Graglia et al. 2001)	Abisko, Sweden	68.35	18.82	10		x		
(Hill and Henry 2011)	Alexandra Fiord, Ellesmere Island, Canada	78.53	-75.55	25	x			
(Hobbie and Chapin 1998)	Toolik Lake, Alaska	68.38	-149.34	3		x		
(Hollister and Webber 2000)	Barrow, Alaska, USA	71.18	-156.4	1				x
(Hollister et al. 2015)	Atqasuk, Alaska	70.45	-157.41	16	x	x		
(Hollister et al. 2015)	Barrow, Alaska	71.29	-156.64	17	x	x		
(Høye et al. 2007)	Zackenberg, Greenland	74.28	-20.34	9			x	
(Hudson and Henry 2009)	Alexandra Fiord, Ellesmere Island, Nunavut	78.88	-75.92	28	x			
(Hudson and Henry 2010)	Alexandra Fiord, Ellesmere Island, Nunavut	78.88	-75.92	16		x		
(Jägerbrand et al. 2009)	Latnjajaure, Lapland, Sweden	68.35	18.5	5		x		
(Jandt et al. 2008)	Northwestern Alaska	65.1	-163.4	10-15	x			
(Joly et al. 2007)	Seward Peninsula, Alaska	64.85	-163.7	25	x			
(Jonasson et al. 1999)	Abisko, Sweden	68.35	18.82	5		x		

(Jones et al. 1997)	Alexandra Fiord, Ellesmere Island, Canada	78.53	-75.55	1					x
(Jones et al. 1997)	Barrow, Alaska, USA	71.19	-156.37	1					x
(Jones et al. 1997)	Latnjajaure, Lapland, Sweden	68.21	18.3	1					x
(Jónsdóttir et al. 2005)	Audkuluheidi, Iceland	65.27	-20.25	5		x			
(Jónsdóttir et al. 2005)	Thingvellir, Iceland	64.28	-21.08	5		x			
(Jorgenson et al. 2015)	Arctic National Wildlife Refuge, Alaska	69.8	-144.25	26	x				
(Marchand et al. 2004)	Zackenberg, Greenland	74.28	-20.34	1					x
(Molau 2010)	Latnjajaure, Lapland, Sweden	68.35	18.5	12	x				
(Myers-Smith et al. 2011b)	Qikiqtaruk-Herschel Island, Yukon	69.57	-138.91	11	x				
(Myers-Smith et al. 2018)	Qikiqtaruk-Hershel Island, Yukon, Canada	69.57	-138.91	16-19	x			x	
(Natali et al. 2012)	Eight Mile Lake, Alaska, USA	63.52	-149.13	2		x			x
(Pattison et al. 2015)	Arctic National Wildlife Refuge, Alaska	69.8	-144.25	26	x				
(Post and Pedersen 2008)	Kangerlussuaq, Greenland	67.6	-50.2	2					x
(Richardson et al. 2002)	Abisko Valley, Sweden	68	19	9		x			
(Robinson et al. 1998)	Ny Alesund, Svalbard	78.93	11.83	5	x	x			
(Rundqvist et al. 2011)	Abisko Valley, Sweden	68.35	18.82	35	x				
(Stenström and Jónsdóttir 1997)	Latnjajaure, Lapland, Sweden	68.22	18.13	1					x
(Tømmervik et al. 2004)	Kautokeino, Norway	69	23.1	38	x				
(Villarreal et al. 2012)	Barrow, Alaska	71.3	-156.67	39	x				
(Vowles et al. 2017)	Ritsem, Sweden	67.824	17.715	18	x				
(Wang et al. 2017)	Kytalyk, Siberia	70.82	147.48	4		x			
(Wilson and Nilsson 2009)	Cievrratjäkka, Sweden	68.01	18.81	21	x				
(Wookey et al. 1993)	Abisko, Sweden	68.21	18.49	1					x
(Zamin et al. 2014)	Daring Lake, NWT	64.87	-111.57	8		x			

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